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THE BUTTERFLY FAUNA OF THE SACRAMENTO VALLEY, CALIFORNIA

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INTRODUCTION

THE STATE OF CALIFORNIA has an extremely rich and varied butterfly fauna, reflecting its topographic, climatic, and botanical diversity (Comstock, 1927; Munz, 1970; Bakker, 1971). The montane faunas, which are perhaps best known, are characterized by a high proportion of endemic species and subspecies. In recent years regional faunas have been published for Sierra Nevada localities: Yosemite National Park (Garth and Tilden, 1963), Mather (Shields, 1966), and Donner Pass (Emmel and Emmel, 1962). A study by Opler and Langston (1968) included both Outer and Inner Coast Ranges in Contra Costa County, as well as part of the Sacramento-San Joaquin Delta. The least well-known butterfly fauna in northern and central California is that of the rather densely populated Sacramento Valley (fig. 1). This is scarcely surprising when the current biotic condition of the Valley is considered. The following discussion is drawn primarily from Thompson (1961) and Sculley (1973), who discussed the climatic, physiographic, and ecological conditions of the pristine and present Valley.

VEGETATION

The vegetation of the Sacramento Valley has been more thoroughly modified by man than that of scarcely any comparably large area in North America. Prior to European-American colonization, three natural communities were widespread in the Valley: bunchgrass-Valley Oak savanna; tule-cattail marsh; and riparian forest (fig. 2). Perennial bunchgrass, with scattered groves of Valley Oak (*Quercus lobata* Nee.), occurred on the higher sites not subject to regular flooding, and was the com-

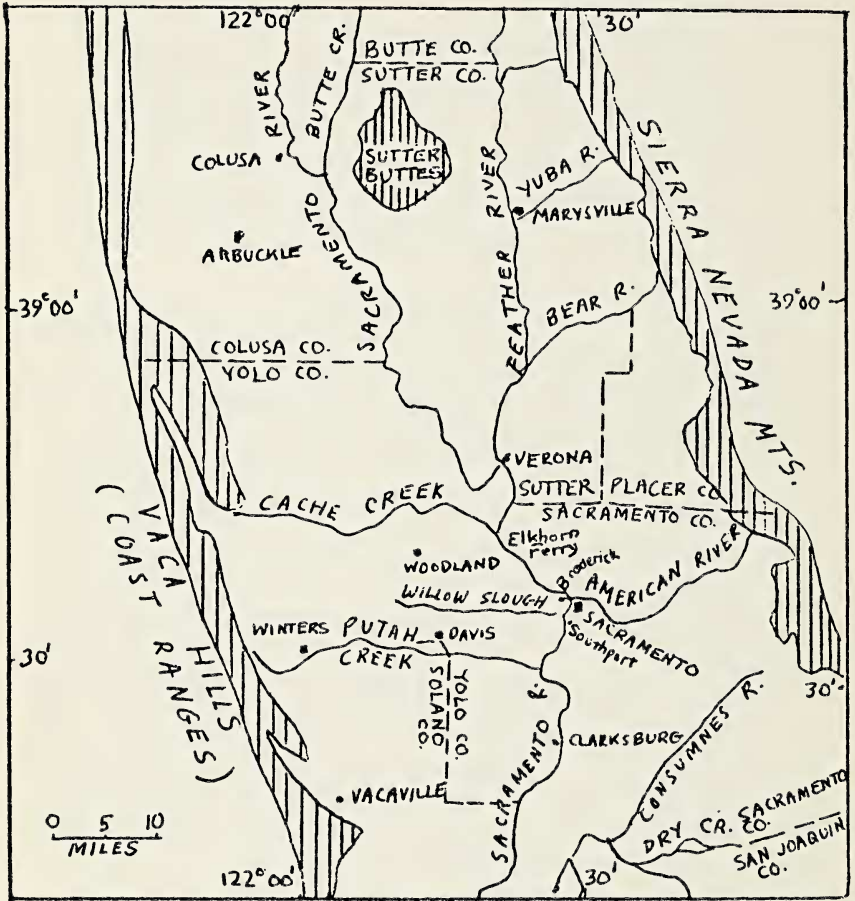
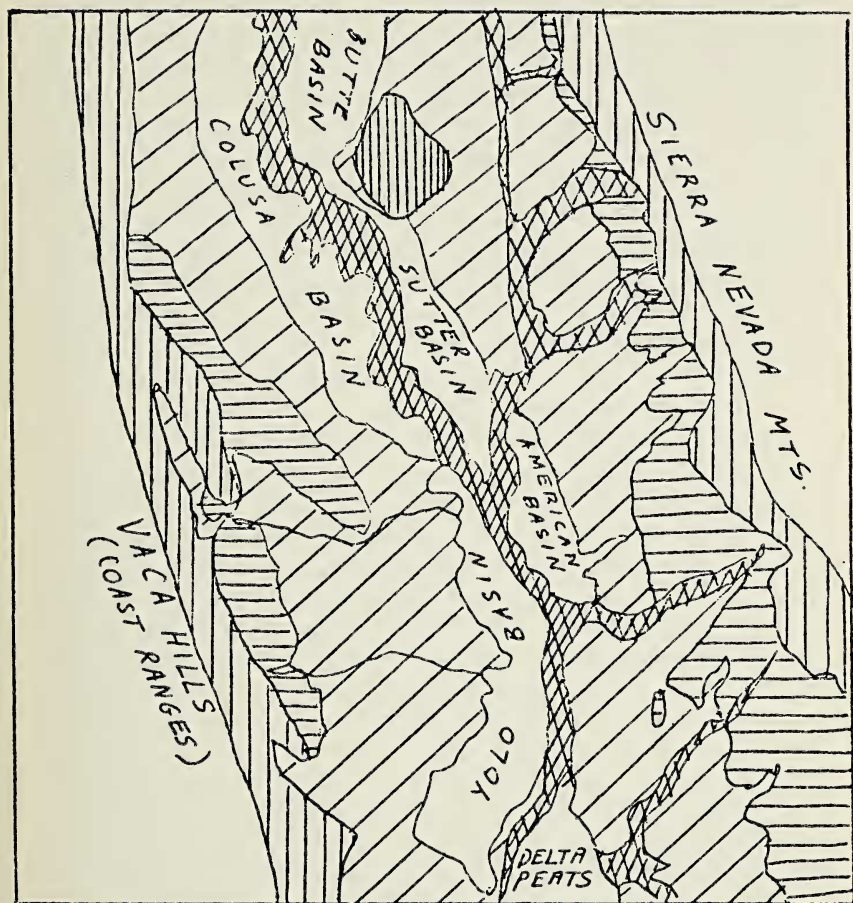



Fig. 1.—Location map of the central Sacramento Valley.



 UPLANDS -
MOSTLY CHAPARRAL

 RED LANDS OR
OLD ALLUVIUM -
OAK & GRASS

 ALLUVIAL PLAINS -
FORMERLY SAVANNA

 RIPARIAN
FOREST &
"NATURAL LEVEES"

 FLOOD BASINS -
FORMERLY TULE
MARSHES

Fig. 2.—Physiographic subdivisions of the central Sacramento Valley, with present biotic communities.

monest vegetation type in the Valley, especially on the west side. The lowlands, which were inundated in normal winters (and in wet years well into summer), supported vast areas of cattails (*Typha*) and common tule (*Scirpus acutus* Muhl.). Torrential rains on the Sierran west slope fed the periodic overflows of the Sacramento River and its tributaries. The major streams built up "natural levees" of silt deposited during flood stages, and these supported a lush deciduous forest dominated by Fremont Cottonwood (*Populus fremontii* Wats.). Deciduousness in a Mediterranean climate like that of California is a luxury which can be afforded only when a reliable year-round supply of ground water is available. The riparian forests of the Sacramento Valley were unique at low elevation in the state.

Of the first two communities little or nothing remains. Most of the bunchgrass prairie was put into pasture or under the plow; either way, the native bunchgrasses were competed out of existence by introduced annual grasses, mostly from Europe. With the bunchgrasses most of the native flora, both annual and perennial, also succumbed, to be replaced by weedy Crucifers, Borages, Mallows, Composites, and other aliens. The marshes were diked or drained and reclaimed for agriculture, or else grossly modified as overflow channels for flood control (the Yolo, Colusa, and Sutter Bypasses). Their original character has in most places been lost. Relict marshlands still exist in West Sacramento and south of Sacramento, at Beach Lake and Stone Lake. Substantial fragments of riparian forest remain in public and private hands—more or less modified by the deletion of native species and the addition of weedy ones, and by restriction in most places to the immediate riverbank where they once had reached 1-4 miles inland.

Little of the Sacramento Valley is free of major ecological disturbance for any significant length of time, and except for the creek bottoms the successional potential of the area—with its radically altered flora—is not really predictable. Most of the former bunchgrass-oak savanna is either intensively farmed or urbanized. The lowland basins are farmed, or farmed in summer and flooded in winter. The riparian forests are under increasing recreational-use pressure, especially from off-road vehicles.

To a casual visitor, the Valley presents a monotonous vegetation due to the ubiquity of early-successional, adventive species. These broadly adapted plants tend to obscure soil and water-table differences which do, however, become apparent in

more mature stands. The lack of native plants and major topographic features, and the constant presence of man tend to discourage butterflies (and Lepidopterists as well). The sandy American River lowland in Sacramento County is mostly not in agricultural use and has the richest butterfly fauna in the Valley, as well as the most mesic vegetation. Thirty-six species—58% of the total Valley fauna—were recorded flying there on June 2, 1973, and the total number of species ever recorded there is 53, or 85% of the Valley fauna. Nonetheless, most of the species are highly vagile and occur in foothill canyons on both sides of the Valley; there is little to necessitate postulating a relict (pre-American) origin for any of the present butterfly populations in the Valley (except perhaps *Phyciodes campestris*).

CLIMATE AND BUTTERFLY PHENOLOGY

Sixty-two species of butterflies have been recorded in the Valley. This is a fairly small fauna by California standards; 134 species are recorded in Yosemite, 84 in Contra Costa County, 74 at Mather (Tuolumne County), about 80 at Donner Pass (Placer County), 70 at Boreal Ridge and 63 at Marin-Sierra Camp, both Nevada County (Shapiro, unpubl.), and about 65 in the east-slope canyons of the Vaca Hills immediately west of the valley (data in part from Shields, pers. comm.). When species which fly into or through the Valley but are not known to breed there are excluded, the fauna drops to 53.

This fauna contrasts strikingly with others in California in the distribution of voltinism. In climates where rainfall is relatively evenly distributed through the year, the proportion of univoltine species increases steadily with elevation and with the shortening of the growing season. In California the summer drought is reflected in the widespread evolution of vernal univoltinism in butterflies at low elevations. The low proportion of univoltines in the Sacramento Valley—only 13% of the resident species (as compared with 39% of the species in the nearby Vaca Hills, Table 1)—reflects the reliable supply of summer water associated with the riparian systems and agricultural irrigation. It also reflects the origins of the fauna, which is largely recruited from the riparian lands where the summer drought has always been less severe than elsewhere.

Relatively few California butterflies are facultatively univoltine; species with only a single brood anywhere generally have only one everywhere, despite considerable altitudinal ranges.

Species which are flexible in brood sequence are primarily lowland colonizers which periodically invade higher elevations but cannot be considered permanent residents there: *Vanessa* spp., *Precis coenia*, *Strymon melinus*, *Lycaena helloides*, *Plebeius acmon*, *Pieris rapae*, *P. protodice*, *Colias eurytheme*, *Pyrgus communis*, *Hylephila phylaeus*. These species are adapted to temporarily unstable habitats, and whatever their geographic origins their seasonal cycles have probably always included up- and downslope colonization. They are the most conspicuous element of the Valley fauna, where they disperse from one disturbed habitat to another in response to agricultural practices. In good years Valley populations probably serve as a source for colonizers which reach the high Sierra.

The climatology of the Sacramento Valley is unusually well documented for the Far West. Reliable records at Sacramento extend back to 1849-50, and recent compilation of means and extremes has been prepared (Figgins, 1971). The Valley has a Mediterranean climate in which rainfall occurs from September to April and is usually concentrated in December, January, and February (see Tables 2 and 3). The Coast Ranges insulate much of the Valley from direct maritime influence and the resulting continentality is shown in the high summer maxima and occasionally low winter minima. The gap in the Coast Ranges at the Carquinez Straits allows a shallow penetration of maritime air in summer which terminates periods of extreme heat after two to four days. Skies are clear in summer, but widespread and persistent low cloudiness and fog prevail in winter and are especially heavy in and near the river bottoms. The highest summer temperatures and the clearest, driest winter weather are provided by "northers," strong northerly winds which develop in response to a north-south pressure gradient and are warmed and dried by their descent from the Siskiyou.

WINTER AND DIAPAUSE STRATEGIES

Sacramento Valley winters are mild and essentially snowless except in the extreme north. Freezes occur up to 30 times each winter, but temperatures below 25°F and continuous freezes of longer than ten hours are exceedingly rare. Under these conditions non-diapausing butterfly immatures may continue their development through the winter. Larvae of *Pieris rapae* from eggs laid in late November develop slowly to pupation in late January at Davis and Woodland. The resulting pupae enter

diapause and eclose in late March or April. Diapausing pupae formed in December or earlier eclose in February and March. A similar winter history is reported for *P. rapae* in England (Gardiner, 1972).

Diapause is generally considered an adaptation to cold winters, and indeed is associated with biochemical defenses against intracellular and extracellular freezing. But in both cold- and mild-winter areas it serves as a timing mechanism correlating spring emergence with the onset of weather suitable for adult activities and—most importantly—likely to be sustained. The limiting factor on butterfly breeding in winter in the Sacramento Valley is the unsuitability of overcast, humid weather for flight activity, regardless of temperature. Persistent fog and low overcast initiate winter in the Valley while temperatures are still relatively high. Winter emergences of Pierid butterflies during fair, mild periods are less common than in the northeastern United States. Spring emergences coincide with decreasing cloudiness and humidity in February and March, and a temperature regime comparable to that in the emergence seasons of the same species in cold-winter areas. Availability of suitable flight weather, rather than nectar sources, seems to be the predominant factor here; major blooms of nectar-rich plants, some native, begin in January in dry years and may continue all winter in wet ones.

The flight season begins several days to two weeks later in the Valley than in the canyons of the Vacas (up to 500 feet). These canyons are sheltered from the spring "northers" which render many otherwise suitable days in the Valley unfit for flight. They also have less fog and dew (which cools the air near the ground and may prevent flight activity most or all of the day if the ambient humidity stays high). The topography of the Valley floor itself also has a bearing on flight times. The American River bottomlands become damp and foggy earlier in fall than the higher ground, and flight activity there ends earlier as a result. During the winter temperatures are moderated by the rapidity with which the air is saturated, and wind velocities (and the desiccating effects of "northers") are braked by the forest cover. Most species emerge four to twelve days earlier in spring at the American River than elsewhere. The local climate there allows *Pieris protodice* to overwinter reliably, something it does only very sporadically in the Valley.

One ecological consequence of the dominance of adventive weeds is the absence of all but a handful of butterfly species

from very extensive tracts of agricultural land. Only one of these is itself adventive from Europe, *Pieris rapae*. Under Valley conditions *rapae* and its primary hosts, *Brassica* spp., are not well-coordinated seasonally. Weedy mustards behave as winter annuals, seldom sustaining much frost damage, and are past their prime when the spring brood of *P. rapae* is peaking. The phenology of alfalfa (*Medicago sativa* L.), the major host of the Orange Sulphur, *Colias eurytheme*, is similar to that of the native perennial legumes on which this butterfly originally fed. *C. eurytheme* overwinters as a third- or fourth-instar dormant (diapausing?) larva.

Hibernating Nymphalid adults generally do not fly on the 10-20 potentially suitable days in winter; they appear in February just before the non-hibernating butterflies. The energetics of Nymphalid hibernation in the mild Sacramento Valley winter is of considerable interest, especially in the Mourning Cloak (*Nymphalis antiopa*) which disappears in early August and remains dormant for six months. Its failure to rear a second brood even along the major rivers is rather perplexing. *Vanessa* (= *Cynthia*) *annabella* departs from the usual pattern of its relatives by overwintering largely as pupae formed in December and early January. Adults alive in December also hibernate successfully, and fresh adults may eclose during warm spells in winter and enter hibernation. This species has been recorded flying 50 weeks of the year at Davis and is the closest thing to a year-round breeder in the Valley. In 1973, when it was abundant, *V. cardui* also bred well into December and continued to eclose.

RAINFALL AND INTERSEASONAL VARIANCE

One of the most striking aspects of Valley climatology is the very high interseasonal variance in rainfall. Temperature characteristics are less variable. Some idea of the variance in precipitation may be obtained from figure 3 and Table 3. The uncertainty of rainfall would be expected to produce adaptations for facultative diapause in species whose host plants are rainfall-dependent. The Papilionid *Battus philenor* produces some diapause pupae in all broods, regardless of photoperiod; these eclose the following spring (rarely fall), with no apparent chilling requirement. *B. philenor* is primarily a foothill species, breeding in canyons where the host plant grows along intermittent

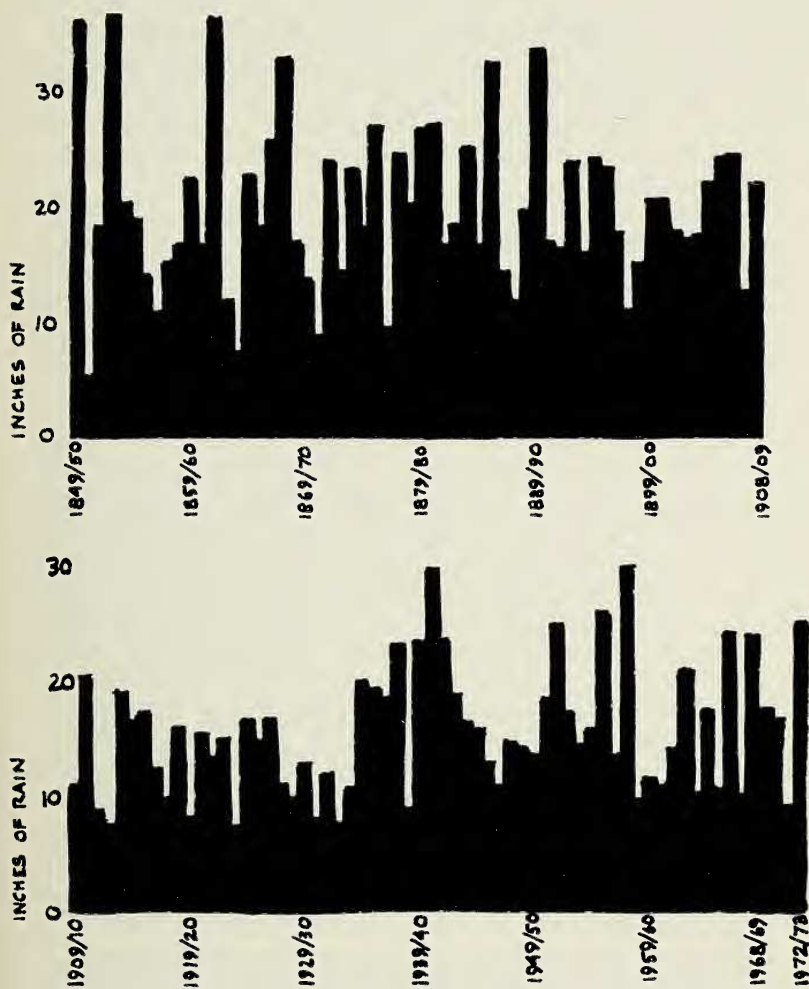


Fig. 3.—Total seasonal rainfall at Sacramento, 1849/50 through 1968/69. From Figgins, 1971.

streams. A similarly mixed developmental strategy occurs in *Euchloe ausonides* and *Anthocharis sara* in the foothills and may be an adaptation to interseasonal variance in rainfall itself, rather than stream flow. On the Sacramento Valley floor, *B. philenor* and *A. sara* are both locally single-brooded, but *E. ausonides* is double-brooded. There is preliminary evidence to suggest that the Davis population of *B. philenor* is genetically univoltine, perhaps reflecting founder effect—sampling error introducing only a portion of the variability of a polymorphic source population.

Dates of spring flights in both univoltine and multivoltine butterflies are well known to be related to weather conditions, both during the emergence season and during the preceding winter. In the Valley, first-flight dates are less variable than in either the Sierra Nevada or upstate New York, both cold-winter areas (cf. Shapiro, 1974a). Even so, dates for the first species, e.g. *Pieris rapae*, may vary several weeks among seasons. Precipitation advances the condition of the vegetation, but overwintering larvae and pupae respond to temperature and perhaps photoperiod. Table 4 presents first-flight dates for 25 common spring butterflies in the Valley after the very dry but mild 1971-72 and very wet and cold 1972-73 winters. Weather data for the two seasons appears in Table 5 and may be compared with the norms in Tables 2 and 3. Although the 1973 flight season began early, continuing episodes of wet and windy weather delayed most species relative to 1972. Emergences in the Vaca canyons were earlier than in the Valley and showed much less departure from 1972 dates, although population levels of many species were quite different in the two years.

Later-emerging species are increasingly insensitive to weather as a determinant of first-flight date. *Satyrium sylvinus*, for example, first appeared v.10 in the Valley in 1973 as against v.15 in 1972 (v.8.72 in the Vacas), but its period of peak numbers was the same both years.

Cutoff dates for flight in autumn are also under meteorological control for the highly multivoltine species. An especially sensitive species is *Papilio zelicaon*. In 1972 it was last recorded on ix.20; in 1973 a full month later, on x.30. That this discrepancy reflects a seasonal difference is well illustrated by data on this species at Suisun Bay, near Fairfield, where the climate is more maritime and *P. zelicaon* normally flies later; in 1972 it was last seen on xi.5 and in 1973 on xi.18.

(Continued on page 115)